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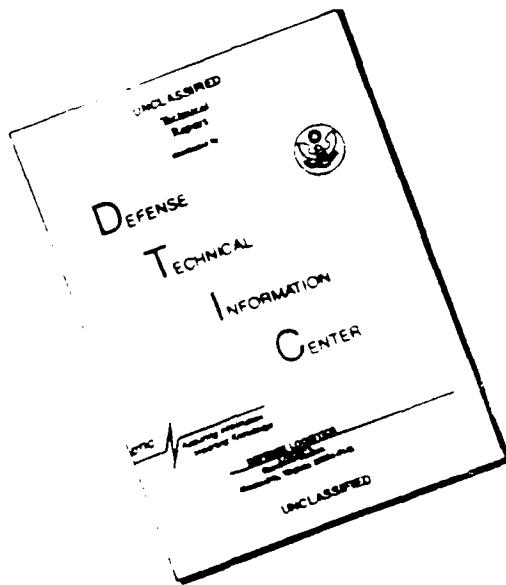
13 ABSTRACT (Maximum 200 words)

We consider the interpretation of time series data from firing events in periodically stimulated sensory neurons. The neurons are represented as nonlinear switching elements embedded in a Gaussian noise background. The cooperative effects arising through the coupling of the noise to the modulation are examined, together with their possible implications in the features of Inter-Spike-Interval Histograms (ISIHs) that are ubiquitous in neurophysiological experimental data. Our approach provides the *simpler* interpretation of the ISIHs and has been found to reproduce the salient features of experimental ISIHs. One such comparison, between very recent data from experiments performed in St. Louis, on the mechanoreceptor in the tailfan of the crayfish *Procambarus clarkii*, and analog simulations on a simple nonlinear excitable neural model is presented to elucidate this point.

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The Role of Noise in Sensory Information Transfer

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ABSTRACT

We consider the interpretation of time series data from firing events in periodically stimulated sensory neurons. The neurons are represented as nonlinear switching elements embedded in a Gaussian noise background. The cooperative effects arising through the coupling of the noise to the modulation are examined, together with their possible implications in the features of Inter-Spike-Interval Histograms (ISIHs) that are ubiquitous in neurophysiological experimental data. Our approach provides the *simplest possible* interpretation of the ISIHs and has been found to reproduce the salient features of experimental ISIHs. One such comparison, between very recent data from experiments performed in St. Louis, on the mechanoreceptor in the tailfan of the crayfish *Procambarus clarkii*, and analog simulations on a simple nonlinear excitable neural model is presented to elucidate this point.

INTRODUCTION

Neuroscientists have known for decades that sensory information is encoded in the intervals between the action potentials or "spikes" characterizing neural firing events. Statistical analyses of experimentally obtained spike trains have shown the existence of a significant random component in the inter-spike intervals. There has been speculation, of late, that the noise may actually facilitate the transmission of sensory information; certainly there exists evidence that noise in networks of neurons can dynamically alter the properties of the membrane potential and the time constants¹. Recent work by Longtin, Bulsara and Moss² (LBM) demonstrated how experimental ISIHs measured, for example, on the auditory nerve fibers of squirrel monkey³ and visual cortex of cat⁴ could be explained via a new interpretation of noise-driven bistable dynamics. They introduced a simple bistable neuron model, a two-state system controlled by a double-well potential with neural firing events corresponding to transitions over the potential barrier (whose height is set such that the deterministic stimulus alone cannot cause transitions). The cell dynamics was described via a variable $x(t)$ loosely denoting the membrane potential and evolving according to

$$\dot{x} = f(x) + Q \sin(\omega t) + F(t), \quad (1)$$

where $f(x)$ is a flow function (expressible as the gradient of a potential $U(x)$) and $F(t)$ is noise, taken to be Gaussian, delta-correlated, with zero mean and variance $2D$. Potentials can be either soft or hard (even infinitely hard) in the bistable description.

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The potential used here was taken to be the "soft" function $U(x) = \frac{1}{2}ax^2 - b\ln(\cosh x)$.

It is instructive to point out that a bistable model of the form (1) can be derived⁵ for the dynamics of more complex networks of neurons and/or dendrites, under certain mean-field-like assumptions. For our analysis, the system (1) is numerically integrated, with the residence time in each potential well (these times correspond to the firing and quiescent intervals) assembled into a histogram, which displays a sequence of peaks with a characteristic spacing. Two unique sequences of temporal measurements are possible: the first measures the residence times in only one of the states of the potential and the histogram consists of peaks located at $t = nT_0/2$, T_0 being the period of the deterministic modulation and n an odd integer. The second sequence encompasses measurements of the total time spent in both potential wells, i.e. it includes the active and refractory or reset intervals; in the presence of noise, the reset intervals are of largely stochastic duration. The histogram corresponding to this sequence consists of peaks at locations $t = nT_0$, where n is any integer. The sequence of peaks implies a form of phase locking of the neural dynamics to the stimulus. Starting from its quiescent state, the neuron attempts to fire at the first maximum of the stimulus cycle. If it fails, it will try again at the next maximum, and so on. The latter sequence is the only one observable in an experiment; the former sequence, which corresponds to the refractory events is elegantly elucidated by the LBM theory. Analog simulations of the dynamics yield an extremely good fit to experimental data; the fit can be realized by changing only one parameter (the stimulus intensity or the noise intensity). In addition to the peak spacing in the ISIH, most of the other substantiative features of experimental ISIHS are explainable via the simple model (1): (a). Decreasing the noise intensity (keeping all other parameters fixed) leads to more peaks in the histogram since the "skipping" referred to above becomes more likely. Conversely, increasing the noise intensity tends to concentrate most of the probability in the first few peaks of the histogram. (b). In general, the probability density of residence times is well approximated by a Gamma distribution of

the form $P(T) = \frac{T}{(T)^2} \exp[-T/(T)]$, where (T) is the mean of the ISIH. It is apparent

that $P(T) \rightarrow 0$ or $\exp(-T/(T))$ in the short and long time limits, respectively. For vanishingly small stimulus amplitude Q , the distribution tends to a Gamma, conforming to experimental observations. (c). Increasing the stimulus amplitude leads to an increase in the heights of the lower lying peaks in the ISIH. (d). Memory effects (even within the framework of a description based on the theory of renewal processes) frequently occur, particularly at very low driving frequencies; they manifest themselves in deviations from an exponentially decaying envelope at low residence times (the first peak in the ISIH may not be the tallest one). (e). The mean of the ISIH yields (through its inverse) the mean firing rate. A more rigorous treatment of the above results is available in recent work⁶; this work also includes comparison of our results with recent experimental data taken from cat auditory nerve. The important point to note here is that the results are almost independent of the functional form of the potential $U(x)$, depending critically on the ratio of barrier height to noise; this ratio determines the hopping rate between the basins of attraction in the absence of noise.

The LBM theory demonstrates that the peaks of the ISIH cannot exist in the absence of noise. Indeed, stimulus cycle skipping, which is necessary to generate a sequence of peaks, cannot occur unless two conditions are fulfilled: there must be noise, and the coherent stimulus must be subthreshold. It also implies the existence of a "regulatory mechanism" in which sensory neurons measure the stimulus amplitude by comparing it to the background noise level, a process that is mediated and optimized by the

(internally adjustable) potential barrier height in the bistable model.

HOW GOOD IS THE BISTABLE DESCRIPTION?

Although the LBM model provides an important first step in the understanding of the (possibly pivotal) role of noise in sensory information transfer, it is far from complete. The results do not depend critically on the characteristics of the potential function $U(x)$ and the fundamental question: what aspects of the data are due to the statistical properties of noisy two-state systems as opposed to properties of cells that transcend this simple description (or, can the neuron be satisfactorily described by a noisy bistable switching element), have still not been satisfactorily answered, although an important first step in this direction is afforded by recent work⁶.

Integrate-fire (IF) models have been exceptionally popular in the quest for a description of the statistical properties of spike trains obtained from excitable cells. For the classical Gerstein-Mandelbrot (GM) model⁷, $f(x) = \mu$, a (positive) constant drift term corresponding roughly to the difference between excitatory and inhibitory post-synaptic potential steps; the dynamics (1) then corresponds to a Wiener process with drift. Other, somewhat more realistic models⁸ assume a decay of the membrane potential, fol-

lowing a firing event, to its resting value; for these models $f(x) = -\frac{x}{\tau} + \mu$ corresponding to Ornstein-Uhlenbeck dynamics. We consider briefly some recent results based on the GM model with deterministic modulation. A simple extension of the original GM calculation leads to a closed form expression of the probability density function of first passage times to an (absorbing) boundary located at a separation a from the starting point. Each crossing of the boundary denotes a firing event which is followed always by a deterministic reset to the starting point, accompanied by perfect phase locking to the periodic stimulus (this is not necessary for the theory; in fact one can assume a random phase ϕ in the argument of the deterministic modulation term in (1), in accordance with what is more common in experiments. Then, averaging over the phase leads to a smoothed ISIH which differs very little from the spontaneous case; we do not discuss this situation here). The solution of the Fokker Planck Equation associated with the deterministically modulated GM model, leads to an analytic computation⁹ of the probability density function of first passage times. This function displays peaks at locations nT_0 , similar to the results obtained from the bistable LBM model (note that this model cannot, however, elucidate the "hidden" symmetry corresponding to the reset events). The peaks are superimposed on a Gamma-like distribution characterizing⁷ the $Q = 0$ case. With increasing inhibition, the density function approaches a Gaussian; the same effect is observed with decreasing noise variance. While the driven IF model reproduces some of the salient features of experimentally observed ISIHS it does not, in general, produce the same excellent agreement with the experimental ISIHS that characterizes bistable models. The formal connection between the two classes of models is also tenuous at present.

We now consider a third class of neuron models; these are the so-called Fitzhugh-Nagumo models corresponding to excitable systems controlled by a bifurcation parameter. In these models, when the membrane voltage variable crosses a boundary, a large excursion (identified as a neural firing event) occurs. This leads to a natural definition of a *deterministic* refractory period, in contrast with the statistical distribution of refractory events that characterizes bistable models. The FHN system is not bistable, but can be made periodically firing or residing on a fixed point, depending on the choice of bifurcation parameter. We write the equations for the model in the form¹⁰:

$$\begin{aligned} \dot{v} &= \nu(v - 0.5)(1 - v) + w + F(t) \\ \dot{w} &= v - w + (b + Q \sin(\omega t)), \end{aligned} \quad (2)$$

where v is the action potential to which noise has been added and w the recovery variable to which the signal is added. The model has been electronically simulated in St Louis, in the fixed point regime ($b = 0.9$) so that bursts of sustained oscillations are absent. Hence one obtains a randomization in the inter-spike intervals, but some coherence with the external signal is maintained. The variable v is treated as the "fast" variable in the dynamics, and its ISIH has been examined in this simulation¹¹. The noise was colored since its correlation time was equal to the time constant of the fast variable but much smaller than the time constant of the slow variable w .

The analog simulator has been described elsewhere and also within this volume¹¹ and so will not be further described here. The fact is that using it we have been easily able to reproduce actual experimental data obtained from periodic stimulation of crayfish mechanoreceptor cells. In order to reproduce the physiological data it is only necessary to set the same signal frequency and then to adjust either the periodic stimulus intensity

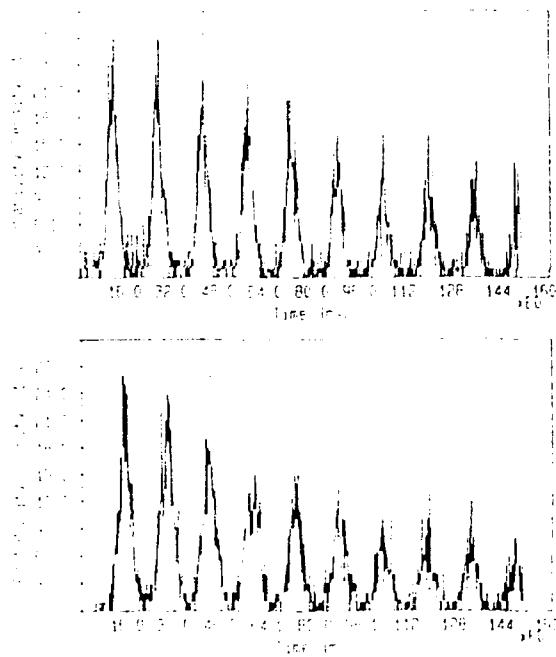


Fig. 1. ISIH's obtained from the crayfish stimulated at 68.6 Hz (upper) and the FHN simulator driven at the same frequency with $b = 0.9$ V; $V_{noise} = 0.022$ V_{rms} , and $V_{sig} = 0.53$ V_{rms} (lower).

or the noise intensity. An example of this is shown in Fig. 1. Moreover, the sharp signal feature, characteristic of additive noise as found in the bistable systems appears in power spectra obtained both from the crayfish and from the FHN model operated

(2)

deeply subthreshold as we have discussed above. The crayfish experiments are described by Douglass, *et al* elsewhere in this volume, and so will not be further detailed here.

DISCUSSION AND CONCLUSIONS

Stochastic resonance is a cooperative nonlinear phenomenon wherein the signal-to-noise-ratio (SNR) of a weak time-varying deterministic signal may be enhanced by the noise; a plot of the SNR vs. noise strength demonstrates a characteristic bell-shaped profile. For low modulation frequencies, the critical value of the noise strength corresponds to a matching between the modulation frequency and twice the Kramers rate. The effect has been extensively analysed¹² and observed in a wide variety of physical systems. It is evident that, in order to take advantage of this effect, there must exist a form of self-regulatory mechanism such that the internal parameters of the system (these parameters control, for instance, the characteristics of the potential function describing bistable systems of the form described earlier in this work) can be adjusted so that it operates close to the maximum of the SNR curve. It is tantalizing to speculate that biological sensory systems might actually routinely utilize this effect for the processing and transmission of information. Our studies of collective behavior in large networks show¹³ that the coupling to other elements can enhance or degrade the SNR depending on the magnitudes and signs of the coupling coefficients (i.e., the excitatory or inhibitory nature of the interactions is critical).

The precise connection between the ISIIs and SR remains somewhat tenuous, although several features of the ISIIs lend themselves to an interpretation based on SR. Perhaps the most important of these features is that the heights of successive peaks (excluding the first) pass through a maximum as a function of the noise strength^{10,14}. ISIIs obtained from the IF models display the same features⁹. So far, attempts to quantify this "resonance" as a matching of two characteristic rates have been inconclusive, largely because of the difficulty of (numerically) producing good ISIIs with low noise. The question of defining a "SNR" from the ISIIs is also largely unanswered.

Experimental investigations into the occurrence of SR in living systems are now underway at at least two laboratories. Douglass, *et al* in this volume and Douglass, Moss and Longtin¹¹ have measured the SNR vs. noise strength curves in the crayfish mechanoreceptor. With externally applied noise, the SNR displays the characteristic bell-shaped response of SR. However, another and inherently more interesting case exists: that wherein the neuron makes use of its own internal noise for subthreshold signal transmission. This question directly relates to the possibility of the existence of an internal noise regulatory mechanism alluded to above and to questions of the evolutionary development of sensory organs using inherently noisy transducers. The experimental difficulty is that the internal neuronal noise is only indirectly controllable, via the temperature of the preparation, for example. For the internal noise case, the results are not as clear. The SNR increases monotonically as a function of the temperature of the saline bath, the crayfish having been acclimated for many weeks in either high or low temperature environments. While there exists an optimal temperature, that is a temperature for which the SNR passes through a maximum, this result does not demonstrate SR using the internal neuronal noise. The reason is that the internal noise *also decreases* beyond the optimal temperature, so that the mechanism which maximizes the SNR at the optimal temperature is different from SR. However, on the low temperature side, the SNR still increases approximately linearly on a logarithmic scale with increasing temperature (internal noise intensity). This result is significant in its own right; it points to the existence of a fundamental nonlinear dynamic mechanism underlying the

cell response. Nevertheless, the dynamics underlying SR seem to be the most likely to provide explanations for the observed effects. These (albeit somewhat, preliminary) results lend credence to our speculations regarding the positive role of noise in the detection and quantification of signals by sensory neurons.

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